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A Parabolic System Modeling Microbial Competition in an Unmixed Bio-reactor

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0. INTRODUCTION

It is well known that two or more microbial populations cannot coexist

which can grow at the lowest nutrient concentration effectively eliminates its rivals from the chemostat. See, for example, [25]. A chemostat is characterized by constant inputs to a well-stirred vessel, and therefore its contents are spatially homogeneous. Several recent studies [3, 9–11, 13, 20, 23–26, 28] have investigated mathematical models of competition for a growth-limiting nutrient in a continuous culture which is not assumed to be well stirred and where the nutrient and populations are assumed to diffuse within the medium in the culture vessel. We will refer to such a bio-reactor as being unmixed (unstirred). The motivation for these studies is that a spatially inhomogeneous environment may allow for coexistence of different populations.

In recent works of Hsu and Waltman [9], Hsu *et al.* [10], and Smith and Waltman [26], a fairly complete mathematical analysis is given of a model of microbial competition for a single limiting nutrient in an unmixed bio-reactor. The model equations take the form of a system of parabolic partial differential equations for the nutrient and competing population concentrations. The main result of these studies is that the model does indeed allow for the possibility of coexistence in the form of a stable equilibrium in which both populations are represented in positive concentration throughout the chemostat under suitable conditions which are stable to small perturbation. Under these conditions, almost all solutions converge to such a positive steady state solution.

The so-called plug flow reactor is a different kind of bio-reactor than that described above (see [21, 22]). Basically, it is a tube through which

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nutrient-containing medium moves at constant velocity. Nutrient and nutrient-consuming microbial populations diffuse and are carried by the flow. Kung and Baltzis [13] have studied a model of competition for a growth-limiting nutrient in the plug flow reactor by constructing various operating diagrams by numerical calculation and simulation which show the existence of steady state solutions as a function of system parameters. Their conclusion is that coexistence can arise via a steady state solution in which both populations are present. A mathematical analysis of a special case of their model was carried out by one of us in [23, 24]. There it is proved that two populations can coexist in a stable equilibrium provided certain conditions hold. If these conditions hold, then almost all solutions converge to a positive (coexistence) equilibrium solution.

Other studies of mathematical models of competition in an unmixed bio-reactor have been carried out by Baxley and Robinson [3], Kirkilonis [11], and Ruan and Pao [20]. These focus primarily on the steady state problem. A common feature of all these studies except for [3] has been the assumption of a common set of boundary conditions for nutrient and competitors. In [9, 10, 26] it is assumed not only that the boundary conditions are identical for all components but also that all the diffusion coefficients are identical. These assumptions appear to be necessary in order that a certain conservation principle holds which allows the elimination of one of the system components, usually the nutrient. This lower dimensional system has strong monotonicity properties which can be exploited to determine the asymptotic behavior of solutions and existence and uniqueness of the various steady states [10, 26]. However, it is unreasonable from a biological point of view to assume that nutrient and various microbial populations diffuse in the medium with the same diffusion coefficient, and consequently it is equally unreasonable that the nutrient and microbial populations should satisfy a common set of boundary conditions. In the present study, we drop these assumptions. The mathematical complications introduced by dropping these assumptions are extensive.

We establish under quite general conditions the existence of a compact global attractor with finite Hausdorff dimension for the dynamical system induced by the equations of our model for m populations of micro-organisms competing for a single growth-limiting nutrient in the unmixed bio-reactor. This result is roughly analogous to the conservation principle for the case where the boundary conditions and diffusion coefficients are identical. It says that the unmixed bio-reactor has a finite carrying capacity for nutrient and biomass. However, in contrast to the earlier studies, this conclusion does not allow the *explicit* reduction of the system to a simpler set of equations. In the remainder of our study, we focus on the steady state solutions which belong to the attractor. Conditions for the existence and uniqueness of single-population equilibria are established, and in the case of two competing microbial populations, we establish sufficient conditions for the existence of a coexistence equilibrium solution. This is an equilibrium in which both populations are simultaneously present in the reactor. Unfortunately, because it is no longer possible to reduce the system to a monotone dynamical system, we are unable to obtain much information about the global asymptotic behavior of solutions as in [10, 26].

The basic model equations, in their simplest form, are formulated in the following section. In addition, the application of our main results to this special case is previewed for the convenience of the reader. In the remaining sections, our main results are proved in a much more general setting.

1. PREVIEW OF MAIN RESULTS

The bio-reactor is assumed to occupy a domain Ω in N-dimensional space (usually, $N=3$) which contains growth medium in which nutrient and microorganisms are suspended. It is an open system in the sense that fresh nutrient is supplied from an external reservoir while growth medium, including unused nutrient and organisms, is removed. This interaction with the external environment occurs at the boundary of Ω, denoted by $\partial\Omega$, and is further described below. Mathematically, this interaction with the external environment is modeled by the boundary conditions. The equations satisfied by nutrient S and the m microbial populations u_i, $1 \leqslant i \leqslant m$, will be assumed here to take the special form:

$$\begin{aligned}\frac{\partial S}{\partial t} &= d_0\, \Delta S - \sum_{i=1}^{m} \gamma_i^{-1} u_i f_i(S)\\ \frac{\partial u_i}{\partial t} &= d_i\, \Delta u_i + u_i(f_i(S) - k_i), \qquad x \in \Omega, \quad t > 0\end{aligned} \tag{1.1}$$

with boundary conditions

$$\begin{aligned}&\frac{\partial S}{\partial \nu}(t, x) + r_0(x)\, S(t, x) = S^0(x)\\ &\frac{\partial u_i}{\partial \nu}(t, x) + r_i(x)\, u_i(t, x) = 0, \qquad x \in \partial\Omega, \quad t > 0,\end{aligned} \tag{1.2}$$

and nonnegative initial conditions

$$\begin{aligned}S(0, x) &= S_0(x)\\ u_i(0, x) &= u_{i0}(x), \qquad x \in \Omega.\end{aligned} \tag{1.3}$$

The constants of proportionality (yield constants), γ_i, between the specific consumption rates in the S-equation and the specific growth rates appearing in the u_i-equation are positive and the $k_i \geqslant 0$ represent cell death rates. $S^0(x) \geqslant 0$ is the important term in the boundary conditions (1.2), reflecting the influx of nutrient at the interface with the reservoir. The functions f_i describe the specific uptake rate of nutrient by the ith population as a function of nutrient concentration. They will be assumed to satisfy:

(i) $f\colon \mathbb{R}_+ \to \mathbb{R}_+$ and $f(0)=0$;

(ii) f is continuously differentiable.

Important examples are the monotone Monod function

$$f(S)=\frac{mS}{a+S}$$

and the non-monotone Andrew's function

$$f(S)=\frac{mS}{a+S+S^2/K}$$

where a, m, $K>0$. Some of our results hold only if the uptake functions are monotone on a suitable interval:

(iii) $f'(S)>0$ for $0 \leqslant S \leqslant L$.

We assume without further mention that (i) and (ii) hold. If a result requires the assumption (iii), then it will be explicitly mentioned along with an appropriate value for L.

The spatial domain Ω is a bounded open connected subset of $\mathbb{R}^N$ with a smooth boundary $\partial\Omega$ and $v=v(x)$ is the outward pointing normal to $\partial\Omega$ at $x \in \partial\Omega$. The partial derivative $\partial/\partial v = v \cdot \nabla$ is the directional derivative in the direction of the outward normal v. The functions $r_i(x)$ and $S^0(x)$ are nonnegative for $x \in \partial\Omega$, do not vanish identically, and are smooth functions. In addition, it is assumed that $\prod r_i(x)$ does not vanish identically. These assumptions reflect the hypothesis that there is a nonzero flux of nutrient into Ω from the reservoir and that there is potentially a nonzero flux of unused nutrient and organism out of Ω if their concentrations become large in Ω.

Although it is not necessary from a mathematical point of view, we imagine that the boundary of Ω is partitioned into three nonempty, pairwise disjoint subsets Γ_i, $i=1, 2, 3$:

$$\partial\Omega = \Gamma_1 \cup \Gamma_2 \cup \Gamma_3.$$

As a motivating example, suppose that Ω is the cylinder $\Omega = D \times (0, L) \subset \mathbb{R}^3$ where D is an open two-disk, $\Gamma_1 = \bar{D} \times \{0\}$, $\Gamma_2 = \bar{D} \times \{L\}$ and $\Gamma_3 = \partial D \times (0, L)$. On Γ_1 there is a steady influx of nutrient (represented by a non-vanishing S^0) into the chamber from an external reservoir and $r_i(x)$ vanish identically. However, no organisms can cross Γ_1. Thus, on Γ_1, the boundary conditions (1.2) are

$$\frac{\partial S}{\partial \nu}(t, x) = S^0(x)$$

$$\frac{\partial u_i}{\partial \nu}(t, x) = 0, \qquad x \in \Gamma_1, \quad t > 0.$$

On Γ_2 there is a steady flux of medium, nutrient and populations out of Ω in proportion to their concentration. Here, $S^0(x) = 0$ so the boundary conditions become

$$\frac{\partial S}{\partial \nu}(t, x) + r_0(x)\, S(t, x) = 0$$

$$\frac{\partial u_i}{\partial \nu}(t, x) + r_i(x)\, u_i(t, x) = 0, \qquad x \in \Gamma_2, \quad t > 0.$$

There is no flux of nutrient or populations across Γ_3. Therefore, $r_i(x) = S^0(x) = 0$ for $x \in \Gamma_3$ and the boundary conditions are

$$\frac{\partial S}{\partial \nu}(t, x) = \frac{\partial u_i}{\partial \nu} = 0, \qquad x \in \Gamma_3, \quad t > 0.$$

We view (1.1)–(1.3) as a semi-dynamical system on $X_+ \equiv \prod_{i=0}^{m} C_+$, where C_+ is the cone of nonnegative functions in the Banach space $C(\bar{\Omega})$ of continuous functions on $\bar{\Omega}$ with the usual supremum norm, $\|\bullet\|$. If $\psi_i \in C$ then we write $\psi_1 \leqslant \psi_2 (\psi_1 < \psi_2)$ whenever $\psi_1(x) \leqslant \psi_2(x)$ $(\psi_1(x) < \psi_2(x))$ for $x \in \bar{\Omega}$.

It turns out to be useful to begin our discussion of (1.1)–(1.3) by considering the so-called washout equilibrium solution in which $u_i = 0$. In practice, attaining this equilibrium is undesireable.

PROPOSITION 1.1. *There exists a unique (washout) equilibrium solution* $S = S_*$, $u_i = 0$ *of* (1.1)–(1.3). S_* *satisfies the boundary value problem*

$$\Delta S_* = 0, \qquad x \in \Omega$$

$$\frac{\partial S_*}{\partial \nu} + r_0(x)\, S_* = S^0(x), \qquad x \in \partial\Omega.$$

Moreover, $S_*(x) > 0$ *for all* $x \in \bar{\Omega}$.

See [26] for the proof of this well known result.

In previous studies, the assumed equalities $r_0 = r_i$, $k_i = 0$ and $d_0 = d_i$, $1 \leqslant i \leqslant m$, lead to an asymptotic conservation principle for (1.1)–(1.3) which shows that solutions are bounded for all time in the norm of X and that there exists a global compact attractor in X. This is accomplished by simply adding the equations in (1.1) to obtain that the sum, $W = S + \sum_i \gamma_i^{-1} u_i$, satisfies the heat equation with inhomogeneous boundary conditions:

$$\frac{\partial W}{\partial t} = d_0 \Delta W$$

$$S^0(x) = \frac{\partial W}{\partial \nu}(t, x) + r_0(x)\, W(t, x)$$

As the corresponding heat equation with homogeneous boundary conditions ($S^0 = 0$) is asymptotically stable, it can be concluded that

$$S + \sum_i \gamma_i^{-1} u_i \to S_*, \qquad t \to \infty,$$

where S_* is as in Proposition 1.1. In particular, S and u_i are bounded in the uniform norm. Furthermore, this analysis allows the elimination of the equation for the nutrient S in (1.1)–(1.3). The resulting reduced system is a monotone dynamical system and as a consequence, a fairly complete analysis of the asymptotic behavior of solutions was made possible [10, 26]. Unfortunately, in the present case, this analysis no longer seems to apply. However, it is still possible to show the existence of a compact global attractor for (1.1)–(1.3) and to get some results on the steady state solutions contained in the attractor.

The following result is a special case of one of our main results. A much more general version holds which does not require the special form of the nonlinearites in (1.1). In fact, the f_i may depend on u_i and the specific growth rate and consumption rates need not be proportional.

THEOREM 1.2. *Equations* (1.1)–(1.3) *generate a semi-dynamical system* $\{T(t)\}_{t \geqslant 0}$ *on* X_+ *which is dissipative and possesses a compact, connected global attractor, A, having finite Hausdorff dimension. If* $(S, u_1, u_2, ..., u_m) \in A$, *then* $0 \leqslant S \leqslant S_*$.

The assertion that (1.1)–(1.3) generates a semi-dynamical system can be paraphrased as follows. Given initial data (1.3) belong to X_+, then the unique solution of (1.1)–(1.3) is defined for $t \geqslant 0$ and remains nonnegative. The maps $T(t)$ are just the translations along a solution given by

$$(S_0, u_{10}, u_{20}, ..., u_{m0}) \to (S(t, \bullet), u_1(t, \bullet), ..., u_m(t, \bullet)).$$

From a biological point of view, the existence of a global attractor says little more than that there is a fixed upper bound on the sizes of the nutrient concentration and the population concentrations which is independent of the initial conditions (1.3). In a sense, the result indicates that the model is realistic, the bio-reactor behaves like a finite planet with finite resources.

The proof of Theorem 1.2 is based on a simple estimate of the sum of the total biomass and nutrient concentration in the chemostat which is not unlike the similar estimate outlined above in the case of equal diffusion coefficients and identical boundary conditions. As the estimate has some biological interpretation, we give it here.

Let $\psi > 0$ be the unit-norm principal eigenfunction of the eigenvalue problem

$$\begin{aligned} -\Delta\psi &= \mu\psi \\ 0 &= \frac{\partial\psi}{\partial\nu} + r\psi \end{aligned} \tag{1.4}$$

where $r(x) = \min\{r_i(x)\colon 0 \leqslant i \leqslant m\}$ and denote by μ the principal eigenvalue. Note that because r does not vanish identically (since $\prod r_i$ doesn't vanish identically), μ is positive. We may view the quantity

$$W(t) = \int_\Omega \psi \left(S + \sum_i \gamma_i^{-1} u_i \right)$$

as a measure of the total amount of nutrient and biomass in the reactor. Multiplying each equation in (1.1) by ψ and integrating over Ω, applying Green's identities, and summing leads to the following equation for W:

$$\begin{aligned} W'(t) &= \int_{\partial\Omega} \left[d_0 S^0 + d_0 S(r - r_0) + \sum_i \gamma_i^{-1} d_i u_i (r - r_i) \right] \psi \\ &\quad - \int_\Omega \left[d_0 \mu S + \sum_i \gamma_i^{-1} (d_i \mu + k_i)\, u_i \right] \psi \\ &\leqslant \int_{\partial\Omega} d_0 S^0 \psi - d\mu W(t) \end{aligned}$$

where $d = \min\{d_i : 0 \leqslant i \leqslant m\}$. As a consequence, we get the L^1-estimate

$$W(t) \leqslant W(0)\, e^{-d\mu t} + (d\mu)^{-1}\,(1 - e^{-d\mu t}) \int_{\partial\Omega} d_0 S^0 \psi.$$

In other words, the total nutrient and biomass in the reactor is bounded on $t \geqslant 0$ and furthermore there is an asymptotic upper bound for it which is independent of the initial data. Of course, in order to prove Theorem 1.2 one must convert this expression of dissipativeness in the L^1 norm to one in the L^∞ norm. This turns out not to be a trivial exercise.

The fact that $S \leqslant S_*$ on the attractor follows immediately from the differential inequality

$$\frac{\partial S}{\partial t} \leqslant d_0\, \Delta S$$

and a standard comparison theorem [27]. See Proposition 2.2 below.

Having established the existence of a compact attractor for (1.1)–(1.3) we now seek to describe the nontrivial steady states: This naturally begins with a consideration of the single-population steady states for which $u_j = 0$ for all except one value of j. For each $i = 1, 2, ..., m$, the eigenvalue problem

$$\begin{aligned} \lambda\phi &= d_i\, \Delta\phi + [f_i(S_*(x)) - k_i]\, \phi, \qquad && x \in \Omega, \\ 0 &= \frac{\partial\phi}{\partial\nu} + r_i(x)\, \phi, && x \in \partial\Omega \end{aligned} \tag{1.5}$$

plays an important role. We denote by λ_i the principal eigenvalue of (1.5). If $\lambda_i > 0$ for some i, then the washout equilibrium is unstable to invasion by the ith population, u_i. The next result implies that the instability condition $\lambda_i > 0$ is a sufficient condition for the existence of at least one single-population steady state with $u_i > 0$. Furthermore, it is also essentially a necessary condition if f_i is monotone, for if $\lambda_i < 0$, then u_i is eliminated from the reactor.

THEOREM 1.3. *If $\lambda_i > 0$ for some i, then* (1.1)–(1.3) *has at least one single-population equilibrium solution $S = \hat{S}_i(x)$, $u_i = \hat{u}_i(x)$, $u_j = 0$ for $j \neq i$. Every such solution satisfies $0 < \hat{u}_i$ and $0 < \hat{S}_i < S_*$. If f_i satisfies* (iii) *with $L = \|S_*\|$ and if $\lambda_i < 0$, then*

$$u_i(t, x) \to 0$$

uniformly in $x \in \Omega$ for every solution of (1.1)–(1.3).

In contrast to the case of equal diffusion coefficients and identical boundary conditions [9, 10, 26], we are unable to conclude the uniqueness of the single-population equilibria, even when f_i is monotone. However, in the special case that the domain Ω is an open subinterval of $\mathbb{R}$ $(N=1)$ we are able to adapt a result of Hsu [8] to obtain uniqueness.

THEOREM 1.4. *Suppose that* $\Omega=(a, b)\subset\mathbb{R}$. *If* f_i *satisfies* (iii) *with* $L=\|S_*\|$ *and if* $\lambda_i>0$, *then there is a unique single-population equilibrium as in Theorem* 1.3.

Finally, assume that there are only two competing populations $(m=2)$ in (1.1)–(1.3). Suppose that $\lambda_i>0$ for $i=1, 2$ so that there are two single-population equilibria $E_1=(\hat{S}_1, \hat{u}_1, 0)$ and $E_2=(\hat{S}_2, 0, \hat{u}_2)$. In fact, we assume that these single-population equilibria are unique. According to Theorem 1.4, this holds in case $N=1$. For $i\in\{1, 2\}$, let μ_i be the principal eigenvalue of

$$\lambda w = d_j\, \Delta w + [f_j(\hat{S}_i) - k_j]\, w$$

$$0 = \frac{\partial w}{\partial \nu} + r_j(x)\, w$$

where $j\neq i$ is the complementary index to i. This eigenvalue problem represents only part of the full variational equation about the single-population equilibrium E_i. Our final result says that if $\mu_i>0$ for $i=1, 2$ or if $\mu_i<0$ for $i=1, 2$, then there is an equilibrium representing the coexistence of the two populations. The condition $\mu_i>0$ $(\mu_i<0)$ simply says that the equilibrium E_i is unstable (stable) to invasion by the complementary population.

THEOREM 1.5. *Let* $m=2$. *If* $\lambda_i>0$ *for* $i=1, 2$ *and if the single-population equilibria* E_i *are both unique and* $\mu_i>0$ *for* $i=1, 2$ *or* $\mu_i<0$ *for* $i=1, 2$, *then there exists an equilibrium solution* $E^*=(S^*, \mu_1^*, \mu_2^*)$ *for which* $u_i^*>0$, $i=1, 2$.

2. THE GLOBAL ATTRACTOR

In this section, general conditions are described which ensure the existence of a compact global attractor. In pursuit of this objective, it is expedient to simplify notation by setting $u_0=S$ and to use vector notation where possible. In particular, we introduce the vector $u=(u_0, u_1, ..., u_m)$, v^0 for the vector whose components are given by the right side of (2.2), and U for the vector of initial conditions in (2.3). Our system cats now be written as

$$\frac{\partial u_i}{\partial t} = d_i\, \Delta u_i + f_i(u), \qquad x\in\Omega, \quad t>0, \quad 0\leqslant i\leqslant m \tag{2.1}$$

with boundary conditions

$$\frac{\partial u_i}{\partial \nu}(t, x) + r_i(x)\, u_i(t, x) = v_i^0, \qquad x \in \partial\Omega, \quad t > 0, \quad 0 \leqslant i \leqslant m \tag{2.2}$$

and nonnegative initial conditions

$$u_i(0, x) = U_i(x), \qquad x \in \Omega, \quad 0 \leqslant i \leqslant m. \tag{2.3}$$

As in the previous section, we assume that the domain $\Omega \subset \mathbb{R}^N$ has a smooth boundary, $\partial\Omega$, and $\nu(x)$ is the outward-pointing normal to $\partial\Omega$ at x. The functions r_i and v_i^0 are nonnegative smooth functions on $\partial\Omega$. In (2.2), we view $v_0^0 = S^0$ and we have allowed for the possibility that there is an influx of bacteria population u_i into the bio-reactor ($v_i^0 > 0$). Moreover, we assume that $r(x) = \min\{r_i(x) : 0 \leqslant i \leqslant m\}$ does not vanish identically. The functions $f_i : \mathbb{R}_+^{m+1} \to \mathbb{R}$ are assumed to be continuously differentiable. The initial data $U \in X_+ \equiv \prod_{i=0}^m C_+$ where C_+ is the cone of nonnegative functions in the Banach space $C(\bar{\Omega})$. The usual supremum norm will be denoted by $\| \bullet \|$. The norm on the Banach space L^p will be denoted by $\| \bullet \|_p$ and, more generally, the norm on the Banach space Y will contain the subscript Y.

Aside from smoothness conditions on the nonlinearities f_i we require that the nonnegative cone $\mathbb{R}_+^{m+1}$ remains positively invariant under the dynamics of (2.1)–(2.3). The following conditions suffice. Biologically, the conditions say that: (i) if no bacteria u_i is present then none can be produced and if no nutrient is present then no consumption of nutrient occurs; (ii) if all bacteria are absent from the bio-reactor then no consumption of nutrient takes place and there are no sources of nutrient in the domain containing the bio-reactor; (iii) if there is no nutrient, then there can be no growth of bacteria. We note that not all of these assumptions are needed for any one result.

(F1) The functions $f_i : \mathbb{R}^{m+1} \to \mathbb{R}$ satisfy:

(i) $f_i(u) = 0$ whenever $u_i = 0$.

(ii) $f_0(u) \leqslant 0$ for all $u \in \mathbb{R}_+^{m+1}$ and $f_0(u_0, 0, ..., 0) = 0$ for $u_0 \geqslant 0$.

(iii) $f_i(0, u_1, ..., u_m) \leqslant 0$ for $1 \leqslant i \leqslant m$.

The following preliminary result just says that corresponding to each initial data $U \in X_+$, there is a unique local solution $u(t, \bullet) \in X_+$ of (2.1)–(2.3) defined for $0 \leqslant t < \tau = \tau(U)$ and that the map $(U, t) \to u(t, \bullet)$ is continuous and satisfies the semi-group property where it's defined. The main goal of this section is to establish sufficient conditions for solutions to be globally defined and for the resulting semi-dynamical system to be point dissipative (see [5]).

PROPOSITION 2.1. *The system* (2.1)–(2.3) *generates a nonlinear local semi-dynamical system on the space* X_+.

Proof. We give only a sketch of this well-known result. Let $u_{i*} \geqslant 0$ be the unique solution of the boundary value problem:

$$\Delta u_i = 0$$

$$v_i^0 = \frac{\partial u_i}{\partial \nu} + r_i u_i$$

See Proposition 1.1. Let $u_* = (u_{0*}, ..., u_{m*})$. The first step is to convert the system to an integral equation for a continuous mild solution u: $[0, \tau) \to X_+$ of

$$u(t) = u_* + B(t)(U - u_*) + \int_0^t B(t-s)\, F(u(s))\, ds$$

where $\{B(t)\}_{t \geqslant 0}$ is the nonexpansive, analytic semigroup on X generated by the closure of the operator $B = \mathrm{diag}(d_i \Delta)$ on an appropriate domain for which the homogeneous Robin boundary conditions hold (i.e., $v^0 = 0$). That is, for $U \in X$, $u = B(t)\, U$ is the unique solution of

$$\frac{\partial u_i}{\partial t} = d_i\, \Delta u_i$$

$$0 = \frac{\partial u_i}{\partial \nu} + r_i u_i$$

$$u_i(0, \bullet) = U_i, \qquad 0 \leqslant i \leqslant m.$$

An important property of the semigroup of operators $B(t)$ is that they are positive operators: $B(t)\, X_+ \subset X_+$. The nonlinear term F: $X_+ \to X$ is defined by $(F(u))(x) = (f_0(u(x)), ..., f_m(u(x)))$. As F is Lipschitz on bounded subsets of X_+ and because (F1) holds, one can show that for each $U \in X_+$ there is a unique solution of the integral equation on a maximal interval of existence $[0, \tau)$, which remains in X_+ (see [15, 16]). The smoothness assumptions on the f_i and the fact that $B(t)$ is an analytic semigroup can be used to show that this solution is a classical solution of (2.1)–(2.3). Furthermore, the map $(U, t) \to u(t)$ is continuous, where $u(t)$ is the solution corresponding to the initial data U, and the semigroup property holds where the map is defined. See [16]. ∎

In order to show that solutions are globally defined we require various estimates of the solutions on their domain of existence. The fact that there are no internal sources of nutrient implies that it is uniformly bounded on the domain of existence. This is stated in the following result. Recall that S_* was defined in Proposition 1.1. By (F1), $(S_*, 0, ..., 0)$ is an equilibrium of (2.1)–(2.2).

PROPOSITION 2.2. *There exists* $K, \sigma > 0$ *such that* $u_0(t, x) \leqslant S_*(x) + K \| U_0 \| e^{-\sigma t}$ *for* $x \in \bar{\Omega}$ *and* $0 \leqslant t \leqslant \tau(U)$.

Proof. Since $f_0 \leqslant 0$, we observe that $w(t, x) = S(t, x) - S_*(x)$ satisfies

$$\frac{\partial w}{\partial t} \leqslant d_0 \, \Delta w$$

$$0 = \frac{\partial w}{\partial \nu} + r_0 w$$

Let ϕ be the unit norm positive principal eigenfunction corresponding to the eigenvalue problem

$$-d_0 \, \Delta \phi = \sigma \phi$$

$$0 = \frac{\partial \phi}{\partial \nu} + r_0 \phi$$

Then $\sigma > 0$ and $W(t, x) = C\phi(x) \, e^{-\sigma t}$ is a solution of the linear parabolic equation corresponding to the inequality above. Letting $C > 0$ be the minimal constant such that $S(0, x) - S_*(x) \leqslant C\phi(x)$, a standard comparison result implies that $w(t, x) \leqslant W(t, x)$ for $x \in \bar{\Omega}$ and $t \geqslant 0$. ∎

In order to show that the bacteria populations are bounded in the future, we require a hypothesis which roughly asserts that growth and consumption are proportional. This implies that, in some sense, the nonlinearities in the system cancel each other so that some linear combination of them has at most linear growth.

(F2) There exist positive constants h_i and real constants k, c such that for all $u \in \mathbb{R}^{m+1}$

$$\sum_{i=0}^{m} h_i f_i(u) \leqslant k \sum_{i=0}^{m} h_i u_i + c. \tag{2.4}$$

Moreover, $k<\mu d$ where $d=\min d_i$ and $\mu>0$ is the principal eigenvalue of

$$\begin{aligned} -\Delta\phi &= \mu\phi \\ 0 &= \frac{\partial\phi}{\partial\nu}+r\phi \end{aligned} \tag{2.5}$$

with $r(x)=\min\{r_i(x)\colon 0\leqslant i\leqslant m\}$.

We begin as in the previous section by showing boundedness of the u_i, $1\leqslant i\leqslant m$, in the L^1 sense.

PROPOSITION 2.3. *Suppose that* (F1) *and* (F2) *hold. Then there are positive constants* C_i, $i=1, 2, 3$ *such that*

$$\begin{aligned} \sum_{i=0}^{m} \|u_i(t,\bullet)\|_1 \leqslant (C_1+C_2\,\|v^0\|)(1-e^{-(\mu d-k)\,t}) \\ +C_3\,\|U\|_1\,e^{-(\mu d-k)\,t} \end{aligned} \tag{2.6}$$

Proof. Let $\psi>0$ be the principal eigenfunction of (2.5). Multiplying the equation for u_i by $h_i\psi$ and integrating over Ω, we obtain

$$\frac{d}{dt}\int_\Omega h_iu_i\psi=\int_\Omega h_i\psi\,\frac{\partial u_i}{\partial t}=d_i\int_\Omega h_i\psi\,\Delta u_i+\int_\Omega h_i\psi f_i(u) \tag{2.7}$$

Using Green's identity, (2.2) and (2.5), we have

$$\begin{aligned} \int_\Omega \psi h_i\,\Delta h_i &= \int_\Omega h_iu_i\,\Delta\psi+\int_{\partial\Omega} h_i\left(\frac{\partial u_i}{\partial\nu}\,\psi-\frac{\partial\psi}{\partial\nu}\,u_i\right) \\ &= -\mu\int_\Omega h_iu_i\psi+\int_{\partial\Omega} h_i\psi(-r_iu_i+v_i^0+ru_i) \\ &\leqslant -\mu\int_\Omega h_iu_i\psi+\int_{\partial\Omega} h_iv_i^0\psi \end{aligned} \tag{2.8}$$

Now set $H(u)=\sum_{i=0}^m h_iu_i$, put (2.8) into (2.7), and add the above inequalities to get

$$\begin{aligned} \frac{d}{dt}\int_\Omega \psi H(u) &\leqslant -\mu d\int_\Omega H(u)\,\psi+\int_\Omega \psi\sum_{i=0}^m h_if_i(u)+\int_{\partial\Omega}\psi\sum_{i=0}^m d_ih_iv_i^0 \\ &\leqslant -\alpha\int_\Omega H(u)\,\psi+C'+C''\,\|v^0\| \end{aligned}$$

where we have also used (2.4) and set $\alpha = \mu d - k$. Integrating the inequality gives

$$\int_\Omega H(u(t,x))\,\psi \leqslant e^{-\alpha t} \int_\Omega H(U)\,\psi + \left(\frac{C' + C''\,\|v^0\|}{\alpha}\right)(1 - e^{-\alpha t})$$

As ψ is positive on $\bar{\Omega}$, (2.6) follows. ∎

Observe that Proposition 2.3 implies the dual estimates

$$\|u_i\|_1 \leqslant C_1 + C_2\,\|v^0\| + C_3\,\|U\|, \qquad t \geqslant 0 \tag{2.9}$$

and

$$\limsup_{t \to \tau(U)} \|u_i\|_1 \leqslant C_1 + C_2\,\|v^0\|. \tag{2.10}$$

Our next hypothesis will allow us to translate these L^1 estimates to L^p estimates for arbitrarily large values of p.

(F3) There exist continuous functions $c_i\colon \mathbb{R}_+ \to \mathbb{R}_+$ such that

$$|f_i(u)| \leqslant c_1(u_0) \sum_{j=1}^{m} |u_j|^\sigma + c_2(u_0), \qquad 1 \leqslant i \leqslant m \tag{2.11}$$

provided $u \in \mathbb{R}_+^{m+1}$, where σ is such that $0 < \sigma < 1 + 2/N$ if $N > 2$ and $\sigma > 0$ if $N \leqslant 2$. (Note: index i and j in the summation do not take the value 0)

An easy consequence of Young's inequality, namely, $|u_i|^p\,|u_j|^\sigma \leqslant d_1(p)\,|u_i|^{p+\sigma} + d_2(p)\,|u_j|^{p+\sigma}$, and (F3) is that for all $p > 0$

$$\sum_{i=1}^{m} |f_i(u)\,u_i^p| \leqslant c_1'(u_0, p) \sum_{i=1}^{m} |u_i|^{\sigma+p} + c_2'(u_0) \tag{2.12}$$

whenever $u \in \mathbb{R}_+^{m+1}$.

The Liapunov-like technique used in the proof below has been used extensively by [1], [17] and [4] to obtain global existence for solutions of parabolic systems. See also page 74 of [6]. we are able to go further in the present context by establishing an asymptotic estimate of the L^p norm of the solution.

Proposition 2.4. *Suppose* (F1), (F2) *and* (F3) *hold. Then, for each* $p > 0$, *there exists a positive continuous function* $C_p(\|U\|)$ *and a positive constant* c_p *such that for* $1 \leqslant i \leqslant m$

$$\|u_i(t, \bullet)\|_p \leqslant C_p(\|U\|), \qquad t \geqslant 0 \tag{2.13a}$$

and

$$\limsup_{t \to \tau(U)} \|u_i(t, \bullet)\|_p \leqslant c_p \tag{2.13b}$$

Proof. Assuming that (2.13) holds for some $p \geqslant 1$ (it holds for $p = 1$ by Proposition 2.3), we shall prove that it holds for exponent $2p$. It is convenient to change variables in (2.1)–(2.3) in such a way that the boundary conditions are homogeneous. Let $z = u - u_*$ where u_* is defined in Proposition 2.1. Then z satisfies

$$\frac{\partial z_i}{\partial t} = d_i \Delta z_i + f_i(z + u_*)$$

and the homogeneous boundary conditions (2.2) (i.e., with $v^0 = 0$). It is easy to see that the map $\hat{f}_i(x, z) \equiv f_i(z + u_*(x))$ satisfies estimates (2.11) and (2.12) where the c_i, c_i' depend only on $z(0, \bullet) \equiv z_0$. Therefore, we will use (2.11) and (2.12) without change in notation. (Of course, the estimates (2.9) and (2.10) have obvious counterparts for the z_i as well.)

For $1 \leqslant i \leqslant m$, multiply the equation for z_i by $z_i |z_i|^{2p-2}$ and integrate to get

$$\int_\Omega z_i |z_i|^{2p-2} \frac{\partial z_i}{\partial t} = d_i \int_\Omega z_i |z_i|^{2p-2} \Delta z_i + \int_\Omega f_i(z + u_*) z_i |z_i|^{2p-2} \tag{2.14}$$

Put $w_i = |z_i|^p$ and note that

$$\int_\Omega z_i |z_i|^{2p-2} \frac{\partial z_i}{\partial t} = \frac{1}{2p} \frac{d}{dt} \int_\Omega w_i^2$$

and

$$\begin{aligned}\int_\Omega z_i |z_i|^{2p-2} \Delta z_i &= \int_{\partial\Omega} z_i |z_i|^{2p-2} \frac{\partial z_i}{\partial \nu} - (2p-1) \int_\Omega |z_i|^{2p-2} |\nabla z_i|^2 \\ &= -\int_{\partial\Omega} r_i |z_i|^{2p} - \frac{(2p-1)}{p^2} \int_\Omega |\nabla w_i|^2 \\ &\leqslant -\frac{(2p-1)}{p^2} \int_\Omega |\nabla w_i|^2 \end{aligned} \tag{2.15}$$

Using these estimates in (2.14), summing over i, and taking into account (2.12) and Proposition 2.2, we find

$$\frac{d}{dt} \int_\Omega \sum_{i=1}^m w_i^2 \leqslant -2d \int_\Omega \sum_{i=1}^m |\nabla w_i|^2 + k_1 \int_\Omega \sum_{i=1}^m w_i^s + k_2 \tag{2.16}$$

where $s=(\sigma+2p-1)/p=2+(\sigma-1)/p$ and k_1, k_2 are positive constants. Note that by (F3), $s<2+2/N$ if $N>2$ so we can apply the Nirenberg–Gagliardo inequality and Young's inequality to see that (see Remark 2.1 and [1])

$$\int_\Omega w_i^s \leqslant \varepsilon \left[\int_\Omega |\nabla w_i|^2 + \left(\int_\Omega w_i \right)^2 \right] + K(\varepsilon) \left(\int_\Omega w_i \right)^q \tag{2.17}$$

for some positive constants q and $K(\varepsilon)$, the latter depending on ε. Choosing $\varepsilon = d/k_1$, from (2.16) and (2.17), there are positive constants l_i such that

$$\frac{d}{dt} \int_\Omega \sum_{i=1}^m w_i^2 \leqslant -d \int_\Omega \sum_{i=1}^m |\nabla w_i|^2 + l_1 \sum_{i=1}^m \left(\int_\Omega w_i \right)^2 + l_2 \sum_{i=1}^m \left(\int_\Omega w_i \right)^q + k_2$$

Applying the Nirenberg–Gagliardo inequality and Young's inequality again in the form

$$\int_\Omega w_i^2 \leqslant d \left[\int_\Omega |\nabla w_i|^2 + \left(\int_\Omega w_i \right)^2 \right] + k_3 \left(\int_\Omega w_i \right)^r,$$

(note the different exponent on w_i than (2.17)) where $r, k_3 > 0$, we obtain from that

$$\begin{aligned} \frac{d}{dt} \int_\Omega \sum_{i=1}^m w_i^2 \leqslant & -\int_\Omega \sum_{i=1}^m w_i^2 + c_1 \sum_{i=1}^m \left(\int_\Omega w_i \right)^2 \\ & + c_2 \sum_{i=1}^m \left(\int_\Omega w_i \right)^q + c_3 \sum_{i=1}^m \left(\int_\Omega w_i \right)^r + k_2, \end{aligned}$$

where the $c_i > 0$. The asserted estimates now follow by applying the induction hypotheses (2.13), noting that $\|z_i\|_p^p = \int_\Omega w_i$ and $\int_\Omega w_i^2 = \|z_i\|_{2p}^{2p}$, and integrating the last inequality. ▮

Remark 2.1. In the Nirenberg–Gagliardo inequality (2.16) we have used the following equivalent norm on $W^{1,2}(\Omega)$ (see [29]):

$$\|u\|_{W^{1,2}(\Omega)} = \left(\int_\Omega |\nabla u|^2 + \left(\int_\Omega u \right)^2 \right)^{1/2}.$$

Remark 2.2. (F2) can be generalized a bit by hypothesizing the existence of functions $h_i \colon \mathbb{R}_+ \to \mathbb{R}_+$ of class C^2 satisfying $h_i'' \geqslant 0$ and $h_i(0)=0$ and

$$\sum_{i=0}^m h_i'(u_i)\, f_i(u) \leqslant k \sum_{i=0}^m h_i(u_i) + c \qquad \text{and} \qquad \sum_{i=0}^m u_i \leqslant c_1 \sum_{i=0}^m h_i(u_i)$$

where k, c satisfy the same hypotheses as in (F2) above and $c_1 > 0$. However, if $v_i^0 \neq 0$ for some i, then we must assume that $h_i'(u_i)$ is bounded for $u_i \geqslant 0$.

THEOREM 2.5. *Suppose that* (F1), (F2) *and* (F3) *hold. Then the solution of* (2.1)–(2.3) *exists for all* $t \geqslant 0$. *Furthermore, there exists a positive continuous function* $K_1(\|U\|)$ *and a positive constant* K_2, *independent of the initial data* U, *such that*

$$\|u_i(t, \bullet)\| \leqslant K_1(\|U\|), \qquad t \geqslant 0 \tag{2.18a}$$

and

$$\limsup_{t \to \infty} \|u_i(t, \bullet)\| \leqslant K_2. \tag{2.18b}$$

Proof. We can regard our problem (2.1)–(2.3) in the larger space $Y = L^p(\Omega)$ in the sense of [19] or [6]. Writing $U(t) = (u_0, u_1, ..., u_m)$ for the solution, we have

$$U(t) = u_* + e^{-At}(U(0) - u_*) + \int_0^t e^{-A(t-s)} F(U(s))\, ds \tag{2.19}$$

where $A = -\operatorname{diag}(d_i \Delta)$, with appropriate (homogeneous) Robin boundary conditions, u_* is as in Proposition 2.1, and $F(U(t)) = (f_0(U(t)), ..., f_m(U(t)))^T$. The semigroup of operators $\{e^{-At}\}_{t>0}$ map Y into the space $Y^\alpha \equiv D(A^\alpha)$ with the graph norm $\|u\|_{Y^\alpha} = \|A^\alpha u\|_p$, where A^α is the fractional power of A (see [19]). We choose p such that $N/2p < \alpha < 1$ and note the imbedding

$$Y^\alpha \to C^\nu, \qquad 0 \leqslant \nu < 2\alpha - N/p \tag{2.20}$$

(see [6]). In particular, $Y^\alpha \subset X$. Furthermore, for each $U \in X_+$, $U(t) - u_* = T(t)\, U - u_* \in C^1(\bar{\Omega}) \cap W^{2,q}_{BC} \subset Y^\alpha$ for $t > 0$, where $q > N$ and the subscript BC means that the homogeneous Robin conditions hold.

Therefore, if $U(0) \in X_+$, $U(t) - u_* \in Y^\alpha$ for $t > 0$. Applying A^α to both sides of (2.19) we have,

$$A^\alpha(U(t) - u_*) = A^\alpha e^{-At}(U(0) - u_*) + \int_0^t A^\alpha e^{-A(t-s)} F(U(s))\, ds.$$

From the L^p estimates of Proposition 2.4 (for all $p \geqslant 1$) and the polynomial growth condition (2.11), we see that there is a positive function

$C = C(\|U\|)$ such that $\|F(U(s))\|_p \leqslant C$ and there is a positive constant c, independent of $\|U\|$, such that

$$\limsup_{t \to \tau(U)} \|F(U(t))\|_p \leqslant c.$$

Therefore, there is a $\eta = \eta(U) > 0$ such that $\|F(U(t))\|_p \leqslant 2c$ for $\eta \leqslant t < \tau(U)$. Consequently, for $t \geqslant \eta$, we have

$$\begin{aligned}
\|U(t) - u_*\|_{Y^\alpha} &= \|A^\alpha(U(t) - u_*)\|_p \\
&\leqslant \|A^\alpha e^{-At}(U(0) - u_*)\|_p \\
&\quad + \int_0^t \|A^\alpha e^{-A(t-s)}\|_{L(Y)} \|F(U(s))\|_p \, ds \\
&\leqslant C_\alpha t^{-\alpha} e^{-\delta t} \|U(0) - u_*\|_p \\
&\quad + \int_0^t C_\alpha (t-s)^{-\alpha} e^{-\delta(t-s)} \|F(U(s))\|_p \, ds \\
&\leqslant C_\alpha t^{-\alpha} e^{-\delta t} \|U(0) - u_*\|_p + \int_0^\eta C C_\alpha (t-s)^{-\alpha} e^{-\delta(t-s)} \, ds \\
&\quad + \int_\eta^t 2c C_\alpha (t-s)^{-\alpha} e^{-\delta(t-s)} \, ds \\
&\leqslant C_\alpha t^{-\alpha} e^{-\delta t} \|U(0) - u_*\|_p \\
&\quad + C C_\alpha \eta t^{-\alpha} e^{-\delta t} + \int_0^\infty 2c C_\alpha r^{-\alpha} e^{-\delta r} \, dr. \qquad (2.21)
\end{aligned}$$

It follows immediately from (2.21) and Theorem 3.3.4 [6] that $U(t)$ is defined for all $t \geqslant 0$ and

$$\limsup_{t \to \infty} \|U(t) - u_*\|_{Y^\alpha} \leqslant 2c C_\alpha \int_0^\infty r^{-\alpha} e^{-\delta r} \, dr.$$

Consequently, we may use the estimate (2.21) and the imbedding (2.20), to conclude that $\tau(U) = \infty$ and that (2.18b) holds.

The estimate (2.18a), for $t \geqslant 1$, follows from the third line of (2.21) by replacing $\|F(U)\|_p$ by C in the integral on the right, using (2.20) and the fact that X imbeds continuously in $L^p(\Omega)$.

In order to see that (2.18a) holds for all $t \geqslant 0$ we need estimates on $0 \leqslant t \leqslant 1$. We can estimate the integral term on the right side of (2.19) in Y^{α} and use (2.20) just as above, so we focus on the part $u_* + e^{-At}(U(0) - u_*) \in X$. But $e^{-At} = B(t)$ (see Prop. 2.1) is nonexpansive on X which leads to the desired estimate on $0 \leqslant t \leqslant 1$. ▮

COROLLARY 2.6. *Let the hypotheses of Theorem 2.5 hold. Then system (2.1)–(2.3) generates a nonlinear semi-dynamical system $T(t): X_+ \to X_+$ having the following properties*:

(a) *$T(t)$ is compact for $t > 0$.*

(b) *$T(t)$ is point dissipative. That is, there exists a bounded set $B \subset X_+$ with the property that for every $U \in X_+$ there is a $\chi = \chi(U) > 0$ such that $T(t)\, U \in B$ for $t \geqslant \chi$.*

(c) *Orbits of bounded sets are bounded. That is $\{T(t)\, C: t \geqslant 0\}$ is bounded for any bounded subset $C \subset X_+$.*

Proof. We notice that in the imbedding (2.20), the uniform norm in (2.18) could be replaced by the C^{ν} norm for some $\nu > 0$. On the other hand, $C^{\nu}(\bar{\Omega})$ is compactly imbedded into $C(\bar{\Omega})$ so we get part (a). We can choose B of part (b) to be the ball in X_+ of radius $2K_2$ where K_2 is the constant in (2.18b). Finally, (c) follows from (2.18a). ▮

We can now state the main result of the section.

THEOREM 2.7. *Let the hypotheses of Theorem 2.5 hold. Then there exists a compact, connected, invariant global attractor A for (2.1)–(2.3) which attracts every bounded set in X_+. Moreover, A has finite Hausdorff dimension. If $u \in A$, then $0 \leqslant u_0 \leqslant S_*$.*

Proof. All but the last-assertion follows from Corollary 2.6 and Theorems 2.8.1 and 3.4.6 in [5]. The last assertion follows from Proposition 2.2. ▮

Theorem 2.7 includes Theorem 1.2 where

$$f_0(u) = -\sum_{i}^{m} \gamma_i^{-1} u_i f_i(u_0)$$

$$f_i(u) = u_i(f_i(u_0) - k_i)$$

It is assumed that the $f_i(u_0)$ appearing on the right side satisfy $f_i\colon \mathbb{R}_+ \to \mathbb{R}_+$ are continuously differentiable functions and $f_i(0)=0$. It is then easy to see that (F1) holds, (F2) holds with $h_0=1$, $h_i=\gamma_i^{-1}$, $1 \leqslant i \leqslant m$, and $k, c=0$, and (F3) holds with $\sigma=1$.

3. EQUILIBRIA

In this section we consider the steady state problem for (2.1)–(2.2) where it is assumed that $v_i^0=0$ for $1 \leqslant i \leqslant m$. The equations are

$$0=d_i\,\Delta u_i+f_i(u), \qquad 0 \leqslant i \leqslant m \tag{3.1}$$

with boundary conditions

$$\begin{aligned} v_0^0 &= \frac{\partial u_0}{\partial v}+r_0 u_0 \\ 0 &= \frac{\partial u_i}{\partial v}+r_i u_i, \qquad 1 \leqslant i \leqslant m. \end{aligned} \tag{3.2}$$

In addition to assuming that (F1)–(F3) hold, we make the following assumption.

(F4) For $1 \leqslant i \leqslant m$, there exist constants $k_i \geqslant 0$ such that $f_i(u)+k_i u_i \geqslant 0$ for $u \in \mathbb{R}_+^{m+1}$.

Without loss of generality we may also suppose that $\partial f_i/\partial u_i(S_*(x), 0, ..., 0)+k_i>0$ for $x \in \bar{\Omega}$, by choosing k_i larger if necessary.

Observe that $u_0=S_*$, $u_i=0$ is an equilibrium solution of (3.1) by virtue of (F1). We refer to it as the "washout equilibrium" denote it by u_*. By Theorem 2.7, every solution u of (3.1) satisfies $u_0 \leqslant S_*$. It is useful to change variables in (3.1) such that the washout equilibrium becomes trivial. Setting $w=S_*-u_0$, equations (3.1) become

$$\begin{aligned} -d_0\,\Delta w &= g_0(x, w, u_1, ..., u_m) \\ -d_i\,\Delta u_i+k_i u_i &= g_i(x, w, u_1, ..., u_m), \qquad 1 \leqslant i \leqslant m \end{aligned} \tag{3.3}$$

together with the homogeneous boundary conditions,

$$\begin{aligned} 0 &= \frac{\partial w}{\partial v}+r_0 w \\ 0 &= \frac{\partial u_i}{\partial v}+r_i u_i, \qquad 1 \leqslant i \leqslant m \end{aligned} \tag{3.4}$$

where

$$g_0(x, w, u_1, ..., u_m) = -f_0([S_*(x) - w]_+, u_1, ..., u_m)$$

$$g_i(x, w, u_1, ..., u_m) = f_i([S_*(x) - w]_+, u_1, ..., u_m) + k_i u_i,$$

for $1 \leqslant i \leqslant m$. The positive part $[S_*(x) - w]_+$ of $S_*(x) - w$ in the first argument of f_i allows an unambiguous interpretation of g_i for all non-negative values of the argument w.

We seek solutions of (3.3)–(3.4) in the cone X_+ of the Banach space X. Of course, in order for a solution of (3.3)–(3.4) to be a solution of (3.1)–(3.2) we must have that $w \leqslant S_*$. For $0 \leqslant i \leqslant m$, let $k_0 = 0$ and k_i be as in (F4) and let K_i: $C(\bar{\Omega}) \to C(\bar{\Omega})$ be the bounded linear operator inverse to $-d_i \Delta + k_i I$, together with the boundary conditions (3.4), where I is the identity. That is, given $h \in C(\bar{\Omega})$, $v = K_i(h)$ is the unique solution of the boundary value problem

$$-d_i \, \Delta v + k_i v = h, \qquad \frac{\partial v}{\partial v} + r_i v = 0.$$

It is well-known (see e.g. [2]) that K_i is a strongly positive, compact operator on $C(\bar{\Omega})$. Equations (3.3)–(3.4) are equivalent to the fixed point problem on X_+ given by

$$U_i = K_i \circ G_i(U), \qquad 0 \leqslant i \leqslant m$$

where, in order to simplify the notation, we have set $U = (w, u_1, u_2, ..., u_m) \in X_+$ and define G_i: $X_+ \to C(\bar{\Omega})$ by

$$G_i(U)(x) = g_i(x, w(x), u_1(x), ..., u_m(x)), \, x \in \bar{\Omega}.$$

To further simplify notation, we write the fixed point equation in vector form

$$U = F(U) \equiv K \circ G(U) \tag{3.5}$$

where $G = (G_0, G_1, ..., G_m)$: $X_+ \to X_+$ (by (F1) and (F4)) and K: $X_+ \to X_+$ is given by $K = \mathrm{diag}\{K_0, ..., K_m\}$. Observe that K is a compact, positive linear operator on X_+ and G is continous on X_+ and satisfies $G(0) = 0$. Therefore, F: $X_+ \to X_+$ is a completely continuous (nonlinear) map. Obviously, $U = 0$ is a fixed point of F; it corresponds to the washout equilibrium of (3.1). we are interested in finding nontrivial fixed points of F in X_+.

PROPOSITION 3.1. *If $F(U) = U$ and $U = (w, u_1, ..., u_m) \neq 0$, then $0 \leqslant w < S_*$ and therefore $u = (S_* - w, u_1, ..., u_m)$ is a solution of* (3.1)–(3.2) *distinct from the washout equilibrium u_*.*

Proof. As $U \neq 0$ is a solution of (3.3)–(3.4), it follows from (F1)(ii) that not all $u_i \equiv 0$, since in that case, $f_0 = 0$ which implies that $w = 0$ so $U = 0$. By (F4), $-d_i \Delta u_i + k_i u_i \geqslant 0$ and so the maximum principle implies that $u_i > 0$ for some i.

In order to show that $u_0 = S_* - w > 0$, it is convenient to work directly with the equation for u_0:

$$-d_0 \, \Delta u_0 = f_0([u_0]_+, u_1, ..., u_m)$$

$$v_0^0 = \frac{\partial u_0}{\partial v} + r_0 u_0$$

Let $s = \inf_{\bar{\Omega}} u_0$ and suppose that $s < 0$ and $u_0(\bar{x}) = s$. If there is such a point $\bar{x} \in \Omega$, let Γ be the connected component of $\{x \in \Omega \colon u_0(x) < 0\}$ containing $\bar{x}$. Then $\Delta u_0 = 0$ in Γ by (F1) so $u_0 \equiv s$ in Γ by the maximum principle. Obviously, this implies that $\Gamma = \Omega$ so $u_0 \leqslant 0$. But then $-d_i \, \Delta u_i \leqslant 0$ for $1 \leqslant i \leqslant m$ by (F1)(iii) and therefore $u_i = 0$ by the maximum principle, a contradiction to the previous paragraph. Thus $\bar{x} \in \partial\Omega$ and there is no such point in Ω. Let Γ be the connected component of $\{x \in \Omega \colon u_0(x) < s/2\}$ containing $\bar{x}$ on its boundary. Again, $\Delta u_0 = 0$ in Γ and since the infimum of u_0, restricted to $\bar{\Gamma}$ is assumed at the boundary point $\bar{x}$ and not in the interior, the boundary point principle states that $\partial u_0 / \partial v(\bar{x}) < 0$. But

$$\frac{\partial u_0}{\partial v}(\bar{x}) = v_0^0(\bar{x}) - r_0(\bar{x}) \, s \geqslant 0,$$

a contradiction. This proves that $u_0 \geqslant 0$. Now it follows by standard maximum principle arguments and the inhomogeneous boundary conditions satisfies by u_0 (see [18, Lemma 4.2, p. 20]) that $u_0(x) > 0$ for all $x \in \bar{\Omega}$. ∎

As the f_i are continuously differentiable functions it follows that F has a derivative $F'_+(0)$ at $U = 0$ in the direction of the cone X_+ (see [2]) and $F'_+(0)$ is a positive, compact linear operator. An easy calculation using (F1) shows that if $\lambda \neq 0$ is an eigenvalue of

$$F'_+(0) \, \Phi = \lambda \Phi$$

for $\Phi = (\psi, \phi_1, ..., \phi_m)$, then λ is an eigenvalue of

$$\begin{aligned} -\lambda d_0 \, \Delta\psi &= -\sum_{i=1}^{m} \phi_i \frac{\partial f_0}{\partial u_i}(S_*(x), 0, ..., 0) \\ -\lambda d_i \, \Delta\phi_i + k_i \lambda \phi_i &= \phi_i \left[\frac{\partial f_i}{\partial u_i}(S_*(x), 0, ..., 0) + k_i \right] \end{aligned} \tag{3.6}$$

for $1 \leqslant i \leqslant m$, with the boundary conditions as in (3.4).

Our principal assumption concerns these eigenvalue problems. It is given immediately below, where, to simplify notation we set

$$a_i(x) = \frac{\partial f_i}{\partial u_i}(S_*(x), 0, ..., 0), \qquad x \in \bar{\Omega}.$$

(E_i) The largest eigenvalue of

$$\begin{aligned} -d_i\, \Delta\phi_i + k_i\phi_i &= \lambda^{-1}[a_i(x) + k_i]\, \phi_i \\ 0 &= \frac{\partial \phi_i}{\partial \nu} + r_i\phi_i \end{aligned} \tag{3.7}$$

is greater than 1. We say that (E) holds if (E_i) holds for $1 \leqslant i \leqslant m$.

Although well suited to the fixed point problem, the form of the eigenvalue problem (3.7) is nonstandard. (E_i) is equivalent to the assumption that the largest (principal) eigenvalue of

$$\begin{aligned} \lambda\phi &= d_i\, \Delta\phi + a_i(x)\, \phi \\ 0 &= \frac{\partial \phi}{\partial \nu} + r_i\phi \end{aligned} \tag{3.8}$$

is positive. Similarly, the largest eigenvalue of (3.7) is less than one if and only if the largest eigenvalue of (3.7) is negative. The proofs of these assertions follow from [2, Theorems 4.3, 4.4 and 4.5] and [12, Theorem 2.5, p. 67] and are well-known.

LEMMA 3.2. *If (E) holds, then one is not an eigenvalue of $F'_+(0)$ corresponding to an eigenvector in X_+ and $F'_+(0)$ has an eigenvalue larger than one with a corresponding eigenvector in X_+.*

Proof. We first note from (3.6) that $(\psi, 0, ..., 0)$ cannot be an eigenvector for $F'_+(0)$ corresponding to a nonzero eigenvalue so if Φ is a positive eigenvector corresponding to $\lambda = 1$, then $\phi_i > 0$ for some i. But this implies that $\lambda = 1$ is the largest eigenvalue of (3.7) for that value of i, a contradiction to (E_i) and the well-known uniqueness of the positive eigenvector. See [2, Theorem 4.3].

On the other hand, let $\lambda_1 > 1$ be the largest eigenvalue of (3.7) corresponding to $i = 1$ and $\phi_1 > 0$ be the corresponding eigenvector and define ψ as the solution of

$$\begin{aligned} -\lambda_1 d_0\, \Delta\psi &= -\phi_1 \frac{\partial f_0}{\partial u_1}(S_*(x), 0, ..., 0) \\ 0 &= \frac{\partial \psi}{\partial \nu} + r_0\psi. \end{aligned}$$

Since $\partial f_0/\partial u_1(S_*(x), 0, ..., 0) \leqslant 0$, by (F1)(ii), and $\phi_1 > 0$ it follows that $\psi \geqslant 0$. Then

$$F'_+(0)(\psi, \phi_1, 0, ..., 0) = \lambda_1(\psi, \phi_1, 0, ..., 0)$$

and since $\lambda_1 > 1$, we are done. ▮

LEMMA 3.3. *There is an $R > 0$ such that*

$$F(U) = \lambda U, \qquad \lambda \geqslant 1 \tag{3.9}$$

has no solution $U \in X_+$ satisfying $\|U\| = R$.

Proof. Equation (3.9) is equivalent to

$$-\lambda d_0\, \Delta w = g_0(x, w, u_1, ..., u_m)$$

$$-\lambda d_i\, \Delta u_i + k_i \lambda u_i = g_i(x, w, u_1, ..., u_m), \qquad 1 \leqslant i \leqslant m$$

together with the boundary conditions (3.4). Arguing exactly as in Proposition 3.1, one finds that $w < S_*$ and therefore $u = (u_0, ..., u_m)$, with $u_0 = S_* - w$, satisfies

$$0 = d_0\, \Delta u_0 + \lambda^{-1} f_0(u)$$

$$0 = d_i\, \Delta u_i + \lambda^{-1} f_i(u) + k_i(\lambda^{-1} - 1)\, u_i$$

together with the boundary conditions (3.2). Define f_λ for $\lambda \geqslant 1$ by $f_\lambda = (\hat{f}_0, ..., \hat{f}_m)$ where $\hat{f}_0 = \lambda^{-1} f_0$ and $\hat{f}_i(u) = \lambda^{-1} f_i(u) + k_i(\lambda^{-1} - 1)\, u_i$, $1 \leqslant i \leqslant m$. Then it is easy to check that if f satisfies (F1)–(F3), which we are assuming, then f and f_λ also satisfy these assumptions with a common set of constants h_i, k, c in (F2) and a common set of functions c_i and exponents σ in (F3), which are independent of $\lambda \geqslant 1$. Consequently, we may take $R = K_2$ where K_2 is defined by (2.18b). ▮

For $r > 0$, let $P_r = \{u \in X_+ : \|u\| < r\}$. We are now in position to make use of the fixed point index (see e.g. [2]).

THEOREM 3.4. *If (E) holds, then there exists r such that $0 < r < R$ and*

$$\mathrm{ind}(F, P_R \backslash \bar{P}_r) = +1,$$

In particular, there is a fixed point of F in $P_R \backslash \bar{P}_r$.

Proof. This is immediate from Lemmas 3.2 and 3.3 and Theorem 13.2i and its proof in [2].

COROLLARY 3.5. *If for some* i, $1 \leqslant i \leqslant m$, (E_i) *holds then there exists a single-population equilibrium of* (3.1)–(3.2) *satisfying* $u_0 = \hat{S}_i$, $u_i = \hat{u}_i$, $u_j = 0$, $j \neq 0, i$, *with* $\hat{u}_i > 0$ *and* $0 < \hat{S}_i < S_*$.

Proof. Assume without loss of generality that $i = 1$. We take $m = 1$ in Theorem 3.4 by dropping the equations for u_j for $j \neq 0, 1$ and setting $u_j = 0$ in the appropriate arguments in f_0 and f_1. Now note that (F1)–(F3) continue to hold for this reduced system. Application of Theorem 3.4 and Proposition 3.1 completes the proof. ∎

Proof of Theorem 1.3. By Corollary 3.5, it remains only to prove the last assertion of Theorem 1.3 so we assume that $f = f_i$ satisfies (iii) with $L = \| S_* \|$, where we are now using the notation in section 1. Suppose that the principal eigenvalue of (1.5) satisfies $\lambda = \lambda_i < 0$. We have dropped the subscript i for simplicity. Then by continuity of the principal eigenvalue to perturbations of the potential, the principal eigenvalue, λ_*, of (1.4), with $S_* + \varepsilon$ replacing S_*, also satisfies $\lambda_* < 0$ provided $\varepsilon > 0$ is sufficiently small. By Proposition 2.2, $S(t, x) < S_*(x) + \varepsilon$ for all large t, say, $t \geqslant T$. Therefore $u = u_i$ satisfies $u_t \leqslant d\, \Delta u + [f(S_* + \varepsilon) - k]\, u$ for $t \geqslant T$. By the comparison principle, as used in the proof of Proposition 2.2, it follows that $u(t, x) \to 0$ at an exponential rate as $t \to \infty$, uniformly in $x \in \Omega$. ∎

We now turn attention to the proof of Theorem 1.5. Here, the focus is on the existence of positive solutions representing coexistence in the case of two competitors ($m = 2$). The equations are (but see Remark 4.1)

$$-d_0\, \Delta S = -\gamma_1^{-1} u_1 f_1(S) - \gamma_2^{-1} u_2 f_2(S)$$

$$-d_1\, \Delta u_1 = u_1[f_1(S) - k_1]$$

$$-d_2\, \Delta u_2 = u_1[f_2(S) - k_2]$$

with the usual boundary conditions. It is assumed that f_i satisfy (i) f_i: $\mathbb{R}_+ \to \mathbb{R}+$ and $f_i(0) = 0$ and (ii) f_i is continuously differentiable. We define $f_i(S) = 0$ for $S \leqslant 0$.

It is assumed that for $i = 1, 2$, the principal eigenvalue of the eigenvalue problem (3.9) is positive. Corollary 3.5 then implies the existence of at least one single-population equilibrium for each of the two populations. One of our main assumptions is that there is exactly one single-population equilibrium for each population and we label these unique solutions as follows:

$$E_1 = (\hat{S}_1, \hat{u}_1, 0), \qquad E_2 = (\hat{S}_2, 0, \hat{u}_2).$$

In Section 4 of this paper it is shown that the uniqueness assumption holds in case $N = 1$ and f_i has a positive derivative on the interval $[0, \| S_* \|]$.

Finally, we assume that the principal eigenvalues of

$$\begin{aligned} \lambda\phi &= d_1\, \Delta\phi + [\, f_1(\hat{S}_2) - k_1\,]\, \phi \\ 0 &= \frac{\partial\phi}{\partial\nu} + r_1(x)\, \phi \end{aligned} \tag{3.11}$$

and of

$$\begin{aligned} \lambda\phi &= d_2\, \Delta\phi + [\, f_2(\hat{S}_1) - k_2\,]\, \phi \\ 0 &= \frac{\partial\phi}{\partial\nu} + r_2(x)\, \phi \end{aligned} \tag{3.12}$$

are either both positive or both negative.

Proof of Theorem 1.5. The proof will make use of the fixed point index and the general approach used in this section. In addition, we exploit the special form of (3.10), particularly, its homogeneity in u_1 and u_2. Note that assumptions (F1)–(F4) are satisfied by (3.10). we consider (3.10) in the form

$$\begin{aligned} -d_0\, \Delta w &= \gamma_1^{-1} u_1 f_1(S_* - w) + t\gamma_2^{-1} u_2 f_2(S_* - w) \\ -d_1\, \Delta u_1 + k_1 u_1 &= u_1 f_1(S_* - w) \\ -d_2\, \Delta u_2 + k_2 u_2 &= u_2 f_2(S_* - w) \end{aligned}$$

where the parameter $t = 1$ and the usual homogeneous boundary conditions hold. More generally, we also consider the homotopy parameter $t \in [0, 1]$. The equivalent fixed point problem will be denoted by

$$U = H(t, U)$$

where $H(1, U) = F(U)$. By a positive solution of (3.10), or equivalently, of $F(U) = U$, we mean a solution for which $u_1 > 0$, $u_2 > 0$. We relabel the single-population fixed points as $E_1 = (\hat{w}_1, \hat{u}_1, 0)$ and $E_2 = (\hat{w}_2, 0, \hat{u}_2)$ where $\hat{w}_i = S_* - \hat{S}_i$.

We will show that either (a) $F(U) = U$ has at least one positive solution in $P_R \backslash \bar{P}_r$, or (b) the fixed point indices satisfy $\operatorname{ind}(F, E_1) = \operatorname{ind}(F, E_2) \in \{0, 1\}$. As $\operatorname{ind}(F, P_R \backslash \bar{P}_r) = 1$ by Theorem 3.4, it follows from the additivity property of the fixed point index that (a) holds if (b) holds. Henceforth, we assume that (a) does not hold. Choose a neighborhood $O = V \times W$ of E_1 in $P_R \backslash \bar{P}_r$ where V is a neighborhood of (w, u_1) in $C(\bar{\Omega}) \times C(\bar{\Omega})$ and W is a small neighborhood of 0 in $C(\bar{\Omega})$ (it does not contain $\hat{u}_2$). Below, we will construct a chain of homotopic mappings and the reader should keep in mind that the domain of each is the neighborhood O.

If there exists $t \in (0, 1]$ such that $H(t, U) = U$ has a solution $U = (w, u_1, u_2)$ on ∂O (relative to X_+), then $u_2 \neq 0$ since otherwise $U = E_1$ by our uniqueness assumption. But E_1 does not belong to the boundary of O. Therefore, $u_2 > 0$ and (w, u_1, tu_2) is a positive fixed point of F, in contradiction to our assumption. If $H(0, U) = U$ has a solution $U = (w, u_1, u_2)$ on ∂O, then $w = \hat{w}$ and $u_1 = \hat{u}_1$. If $u_2 = 0$, then $U = E_1$ but the latter does not belong to ∂O. Therefore, $u_2 > 0$ by the maximum principle and consequently we have a contradiction to our assumption that the principal eigenvalue of (3.12) is not zero. We conclude that $H(t, U) = U$ has no solutions (t, U) with $0 \leqslant t \leqslant 1$ and $U \in \partial O$. Consequently, by the homotopy invariance of the degree

$$\operatorname{ind}(F, E_1) = \operatorname{ind}(H(1, \bullet), E_1) = \operatorname{ind}(H(0, \bullet), E_1).$$

We have effectively decoupled the equations.

Now consider the boundary value problem with parameter $t \in [0, 1]$ given by

$$\begin{aligned} -d_0\, \Delta w &= \gamma_1^{-1} u_1 f_1(S_* - w) \\ -d_1\, \Delta u_1 + k_1 u_1 &= u_1 f_1(S_* - w) \\ -d_2\, \Delta u_2 + k_2 u_2 &= u_2 f_2(S_* - [tw + (1-t)\, \hat{w}_1]) \end{aligned} \tag{3.13}$$

In fixed point form, (3.13) becomes

$$G(t, U) = U.$$

If $G(t, U) = U$ for some $t \in [0, 1]$ and $U = (S, u_1, u_2) \in \partial O$, then obviously $w = \hat{w}_1$ and $u_1 = \hat{u}_1$ so $u_2 = 0$ by our assumption concerning the principal eigenvalue of (3.12). Thus $U = E_1$ which does not belong to the boundary of ∂O. Again, by the homotopy invariance of the degree,

$$\operatorname{ind}(F, E_1) = \operatorname{ind}(H(0, \bullet), E_1) = \operatorname{ind}(G(1, \bullet), E_1) = \operatorname{ind}(G(0, \bullet), E_1).$$

However, $G(0, \bullet)$ can be viewed as the product of two maps G_1 on V and G_2 on W, which are associated with the boundary value problems

$$\begin{aligned} -d_0\, \Delta w &= \gamma_1^{-1} u_1 f_1(S_* - w) \\ -d_1\, \Delta u_1 + k_1 u_1 &= u_1 f_1(S_* - w) \end{aligned}$$

and

$$-d_2\, \Delta u_2 + k_2 u_2 = u_2 f_2(S_* - \hat{w}_1)$$

respectively, with the obvious boundary conditions. Now,

$$\operatorname{ind}(G_1, V) = +1$$

by applying Theorem 3.4 to the case $m = 1$ as in Corollary 3.5 and using the uniqueness of E_1. Furthermore, if the principal eigenvalue of (3.12) is positive, then

$$\text{ind}(G_2, W_+) = \text{ind}(G_2, 0) = 0$$

where W_+ is the intersection of the neighborhood W with the positive cone in $C(\bar{\Omega})$. In fact, this assertion follows from Lemma 13.1(ii) of [2] where we note that the positive, compact linear map G_2: $C_+(\bar{\Omega}) \to C_+(\bar{\Omega})$, given by $G_2(u_2) = K_2[u_2 f_2(S_* - \hat{w}_1)]$, does not have one as an eigenvalue corresponding to an eigenvector in $C_+(\bar{\Omega})$ by virtue of our assumption concerning the principal eigenvalue of (3.12). Indeed, the latter implies that G_2 does have an eigenvalue larger than one with a corresponding positive eigenvector (see the remarks following (3.7)). On the otherhand, if the principal eigenvalue of (3.12) is negative, then

$$\text{ind}(G_2, 0) = +1$$

by Lemma 13.1(i) of [2] since the spectral radius of G_2 is smaller than one (see remarks following (3.7)).

By the product theorem of Leray (Theorem 13.F in [29]),

$$\text{ind}(G(0, \bullet), E_1) = \text{ind}(G_1, V)\,\text{ind}(G_2, 0).$$

The product is either 0 or 1 depending on whether the principal eigenvalues of (3.11) and (3.12) are both positive or both negative. In either case, the fixed point index of F on $P_R \backslash \bar{P}_r$ is not the sum of the indices at the two fixed points E_1 and E_2. By the additivity property of the fixed point index, there must be another fixed point of F and by standard maximum principle arguments together with the uniqueness of the single-population equilibria, any such fixed point must be a positive fixed point of F in $P_R \backslash \bar{P}_r$, a contradiction.

Remark 3.1. Theorem 1.5 can be generalized to allow the $\gamma_i^{-1} f_i$ appearing in the first of equations (3.10) to be replaced by functions $g_i(S)$ having the same properties as f_i. In this case, further assumptions are necessary in order that (F1)–(F3) hold.

4. UNIQUENESS OF SINGLE-POPULATION EQUILIBRIA

In this section we shall give the proof of Theorem 1.4. The essential idea is adapted from a result of [8]. We consider the following boundary value problem

$$\begin{aligned} S'' &= uf(S) \\ u'' &= -ug(S), \qquad 0 < x < 1, \end{aligned} \tag{4.1}$$

with boundary conditions

$$\begin{aligned} -S'(0)+r_0(0)\,S(0)&=c_0 \qquad & -u'(0)+r_1(0)\,u(0)&=0 \\ S'(1)+r_0(1)\,S(1)&=c_1 \qquad & u'(1)+r_1(1)\,u(1)&=0 \end{aligned} \tag{4.2}$$

where $f\colon \mathbb{R}_+ \to \mathbb{R}_+$ and $g\colon \mathbb{R}_+ \to \mathbb{R}_+$ are increasing continuously differentiable functions on the interval $[0, \|S_*\|]$ satisfying $f(0)=0$ and $g(0)=0$, $r_i(x) \geqslant 0$, $i=1, 2$, $x=0, 1$ and $r_0(0)+r_0(1)>0$ and finally, $c_i \geqslant 0$, $c_0+c_1>0$. Recall that $S_*(x)$ is the unique solution of

$$S''=0, \qquad -S'(0)+r_0(0)\,S(0)=c_0, \qquad S'(1)+r_0(1)\,S(1)=c_1.$$

A simple calculation implies that

$$\|S_*\| = \frac{c_1+c_0+\max\{c_0 r_0(1), c_1 r_0(0)\}}{r_0(1)+r_0(0)+r_0(0)\,r_0(1)}.$$

Theorem 1.4 will follow from the following.

PROPOSITION 4.1. *There is at most one solution of* (4.1) *satisfying* $u(x)>0$ *and* $0<S(x)\leqslant \|S_*\|$ *for* $0 \leqslant x \leqslant 1$.

A sequence of lemmata facilitates the proof of Proposition 4.1.

LEMMA 4.2. *Let* (S_1, u_1) *and* (S_2, u_2) *be solutions of* (4.1) *satisfying the conditions of Proposition* 4.1. *If* $S_1 \geqslant S_2$ *on* $(0, 1)$, *then* $(S_1, u_1)=(S_2, u_2)$.

Proof. Multiply the equation for u_1 by u_2 and the equation for u_2 by u_1, subtract and integrate, to get

$$\int_0^1 u_1 u_2 (g(S_1)-g(S_2))\,dt = (u_2' u_1 - u_2 u_1')(1) - (u_2' u_1 - u_2 u_1')(0) = 0$$

where the last equality is due to the boundary conditions. Taking into account that $u_i>0$, $S_i \geqslant S_j$ on (0,1) and the monotonicity of g, we conclude that $S_i = S_j$ on $[0, 1]$. As $f(S_i)>0$, we conclude from the first of equations (4.1) that $u_1=u_2$ on $[0, 1]$. ∎

Hereafter, we assume that (S_1, u_1) and (S_2, u_2) are distinct solutions of (4.1) satisfying the conditions of Proposition 4.1. By Lemma 4.2, $S_1(x) = S_2(x)$ must hold for some (but not all) $x \in (0, 1)$.

LEMMA 4.3. *The functions* $S_1(x)$ *and* $S_2(x)$ *can agree at at most finitely many points of* $(0, 1)$.

Proof. The proof follows [8]; we reproduce it here for the convenience of the reader. From Lemma 4.2, $S_1 - S_2$ must change sign on (0,1). Suppose that $S_1(x) = S_2(x)$ for an infinite sequence of distinct points $\{x_n\} \in [0, 1]$. By compactness, we can assume that there is an $a \in [0, 1]$ such that $x_n \to a$, by passing to a subsequence if necessary. By the mean value theorem applied to $S = S_1 - S_2$, we conclude that $S_1^{(j)}(a) = S_2^{(j)}(a)$ for $j = 0$, 1, 2, 3. Because $S_i > 0$ and $f(S_i) > 0$ on $[0, 1]$, the first equation of (4.1) gives $u_1(a) = u_2(a)$ and the second gives $u_1''(a) = u_2''(a)$. Differentiating the first equation of (4.1) gives also $u_1'(a) = u_2'(a)$. Now by uniqueness of solutions of initial value problems, $(S_1, u_1) = (S_2, u_2)$. ∎

By Lemmas 4.2 and 4.3, there is an $n \geqslant 2$ and points x_i satisfying $1 = x_0 < x_1 < \cdots < x_n = 1$ such that $S_1(x) - S_2(x)$ changes sign at x_i for $1 \leqslant i \leqslant n-1$. We assume that there are no other sign changes of $S_1 - S_2$. Note that on each interval (x_k, x_{k+1}), $S_1 - S_2$ can vanish only finitely many times. Without loss of generality, we assume that $S_1 \geqslant S_2$ on (x_k, x_{k+1}) for even values of k and the reverse inequality holds when k is odd. Hereafter, i and j are assumed to be distinct elements of $\{1, 2\}$.

LEMMA 4.4. *Let $k \in \{1, 2, ..., n-2\}$ and assume that $S_i \geqslant S_j$ on $[x_k, x_{k+1}]$. Then $u_i(x) < u_j(x)$ holds for some $x \in (x_k, x_{k+1})$.*

Proof. Let $a = x_k$ and $b = x_{k+1}$. If $u_i \geqslant u_j$ on (a, b), then using $S_i(a) = S_j(a)$ and $S_i'(a) \geqslant S_j'(a)$ and that f is increasing, we get

$$S_i(b) = S_i(a) + S_i'(a)(b-a) + \int_a^b \int_a^t u_i(s)\, f(S_i(s))\, ds\, dt$$

$$> S_j(a) + S_j'(a)(b-a) + \int_a^b \int_a^t u_j(s)\, f(S_j(s))\, ds\, dt = S_j(b),$$

where the strict inequality results from the fact that $f(S_i) > f(S_j)$ except at finitely many points. The inequality produces a contradiction to $S_i(b) = S_j(b)$. ∎

LEMMA 4.5. *If $S_i \geqslant S_j$ on $[x_k, x_{k+1}]$ and if there exists $c \in [x_k, x_{k+1}]$ such that $u_j(c) \geqslant u_i(c)$ and $u_j'(c)\, u_i(c) - u_j(c)\, u_i'(c) \geqslant 0$, then $u_j \geqslant u_i$ on $[c, x_{k+1}]$.*

Proof. Multiplying the equation for $u_i(u_j)$ by $u_j(u_i)$, subtracting and integrating over the interval $[c, x] \subset [c, x_{k+1}]$, we find that

$$u_i^2 \left(\frac{u_j}{u_i}\right)'(x) = (u_j' u_i - u_j u_i')(x) = \int_c^x u_i u_j (g(S_i) - g(S_j))\, dt$$
$$+ (u_j' u_i - u_j u_i')(c) \geqslant 0 \tag{4.3}$$

This implies that u_j/u_i is nondecreasing on $[c, x_{k+1}]$. As $u_j(c) \geqslant u_i(c)$, the result follows. ∎

Proof of Proposition 4.1. We show that there is some index $m \in \{0, 1, ..., n-1\}$ such that $S_i \geqslant S_j$ on $[x_m, x_{m+1}]$ and $u_i(x_m) \geqslant u_j(x_m)$ where $i = 1$ if m is even and $i = 2$ if m is odd. Since $S_1 \geqslant S_2$ on $[x_0, x_1]$, we are done if $u_1(x_0) \geqslant u_2(x_0)$ since then $m = 0$ works. If $u_1(x_0) < u_2(x_0)$, then the boundary conditions for u at x_0 imply that we may use Lemma 4.5 to conclude that $u_2 \geqslant u_1$ on $[x_0, x_1]$. So $u_2(x_1) \geqslant u_1(x_1)$ and $S_2 \geqslant S_1$ on $[x_1, x_2]$ and $m = 1$ works.

Next we show that if $S_i \geqslant S_j$ on $[x_m, x_{m+1}]$ and $u_i(x_m) \geqslant u_j(x_m)$ and if $m < n-1$, then $u_j(x_{m+1}) \geqslant u_i(x_{m+1})$ and, of course, $S_j \geqslant S_i$ on $[x_{m+1}, x_{m+2}]$. Indeed, by Lemma 4.4, there is a point $c \in (x_m, x_{m+1})$ such that $u_i(c) < u_j(c)$. If $\hat{c} = \inf\{c \in [x_m, x_{m+1}]: u_i(c) < u_j(c)\}$, then it is not hard to see that we must have $u_i(\hat{c}) = u_j(\hat{c})$ and $u_i'(\hat{c}) \leqslant u_j'(\hat{c})$. Lemma 4.5 can then be applied to show that $u_j \geqslant u_i$ on $[\hat{c}, x_{m+1}]$. In particular, $u_j(x_{m+1}) \geqslant u_i(x_{m+1})$ and we are done. Hence, by induction we have these inequalities for indices $m, m+1, ..., n-1$.

On $[x_{n-1}, x_n]$, we have $S_i \geqslant S_j$ and $u_i(x_{n-1}) \geqslant u_j(x_{n-1})$ where i depends on the parity of n. We now want to show that there exists a $c \in (x_{n-1}, x_n)$ such that $u_i(c) < u_j(c)$. Note that the argument using Lemma 4.4 cannot be used for this since we do not necessarily have $S_i(x_n) = S_j(x_n)$. Suppose that $u_i \geqslant u_j$ on $[x_{n-1}, x_n]$. Then $S_i(x_{n-1}) = S_j(x_{n-1})$ and $S_i'(x_{n-1}) \geqslant S_j'(x_{n-1})$ and therefore

$$S_i'(x_n) = S_i'(x_{n-1}) + \int_{x_{n-1}}^{x_n} u_i f(S_i)\, dt > S_j'(x_{n-1}) + \int_{x_{n-1}}^{x_n} u_j f(S_j)\, dt = S_j'(x_n).$$

But this contradicts the boundary conditions at $x_n = 1$. In fact

$$S_i'(1) = c_1 - r_0(1)\, S_i(1) \leqslant c_1 - r_0(1)\, S_j(1) = S_j'(1)$$

where we have used that $S_i \geqslant S_j$ on $[x_{n-1}, 1]$. Therefore, there must exist c as asserted above. Defining $\hat{c}$ exactly as in the previous paragraph, we must have $u_i(\hat{c}) = u_j(\hat{c})$ and $u_j'(\hat{c}) \geqslant u_i'(\hat{c})$ and therefore, by Lemma 4.5 again, that $u_j \geqslant u_i$ on $[\hat{c}, 1]$. But then putting $x = 1$ in (4.3) and using the boundary conditions, we obtain

$$0 = (u_j' u_i - u_j u_i')(1) = \int_{\hat{c}}^{1} u_i u_j (g(S_i) - g(S_j))\, dt + (u_j' u_i - u_j u_i')(\hat{c}) > 0.$$

This contradiction completes the proof of Proposition 4.1. ∎

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